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CROSSDATING DEAD TREES: DOES SAMPLING HEIGHT INFLUENCE RESULTS?

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ABSTRACT

In trees experiencing stress prior to death, growth may be partially or totally suppressed, or may occur only in the upper part of the boles. This may induce inaccuracies when retrospectively crossdating dead trees. In this study, we investigated the occurrence and range of time lags between year of last ring production (YOLRP) in crossdated discs collected at the base, at breast height (BrH), and in the upper part (UP) of the boles of 145 snags and logs of four boreal species. We also assessed the influence of tree age and growth prior to death. When comparing YOLRP in the upper and lower part of trees, more than half the time lags departed from zero. Mean lags ranged from 0.6 to 4.6 years according to species, with lags up to 14 years. Negative time lags, *i.e.* ring production occurring in the lower part of boles while it has stopped in the upper part, were also observed in up to 26% of cases. We suggest that when reconstructing fine patterns of mortality where accuracy must be optimized, sampling entire discs at BrH should be considered, as well as sampling a disc in the UP when sampling old or slowly declining trees.

Keywords: Dendrochronology, crossdating, missing rings, dead trees, year of death, time lag, *Populus tremuloides*, *Abies balsamea*, *Pinus banksiana*, *Picea mariana*

INTRODUCTION

Application of dendrochronological crossdating to date year of death of dead trees is commonly used in forest ecology, especially in retrospective studies. This technique has been used in (1) studying spatial (Rouvinen *et al.* 2002; Aakala *et al.* 2007) and temporal (Mast et Veblen 1994; Cherubini *et al.* 2002; Rouvinen *et al.* 2002; Aakala *et al.* 2009) patterns of mortality, (2) forest dynamics and historical reconstruction of stands (Lorimer and Frelich 1989; Bosch and Gutiérrez 1994; Bergeron 2000; Stan *et al.* 2011), (3) dead trees dynamics and degradation (Johnson and Greene 1991; Daniels *et al.* 1997; Aakala *et al.* 2008; Angers *et al.* 2010, 2012a,b) and (4) impact of biotic agents such as insect outbreaks (Morin 1994; Simard and Payette 2001) or abiotic agents such as droughts (Pedersen 1998, Bigler 2007), fire (Bergeron and Charron 1994) and windthrows (Dynesius and Jonsson 1991).

The use of tree-ring analysis to estimate year of tree death, however, has its shortcomings. Year of death is generally assumed to be the year of last ring production (YOLRP) but sources of errors can be caused by the degradation state of samples (decay or erosion of the outermost rings) and by early interruption of ring production before death.

Premature interruption of growth occurs when all photosynthates are directed to vital functions such as maintenance of photosynthetic tissues, fine roots, and reproductive structure production, so that very few or no resources are available to allow secondary growth (Waring and Pitman 1985; Oliver and Larson 1990). In these cases, there is a delay between the YOLRP and the observed death

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of trees, *i.e.* when trees lack green foliage. This delay can only be quantified by contrasting direct field observations and dendrochronological crossdating (Mast and Veblen 1994; Cherubini *et al.* 2002; Jones and Daniels 2012).

Growth can also be interrupted locally and induce anomalies in ring formation. This partial cambial mortality can translate into incomplete production of rings around the whole circumference of a tree at a given height (Amoroso and Daniels 2010; Stan *et al.* 2011; Jones and Daniels 2012; Bigler and Rigling 2013). Because cambial activity is initiated by growth hormones in apical zones, growth can also vary along the stem, with rings produced only in the higher portion of the tree while no growth trace is left in the lowermost part (Bormann 1965; Kolishchuk 1990; Novak *et al.* 2011). Growth anomalies are particularly observed in stressed trees that are suppressed, wounded, declining, slowly growing, or very old (Bormann 1965; Johnson and Greene 1991; Lorimer *et al.* 1999; Amoroso and Daniels 2010; Stan *et al.* 2011; Jones and Daniels 2012), experiencing climatic stress such as drought (Kozlowski and Pallardy 1997; Bigler *et al.* 2007; Novak *et al.* 2011) or biotic disturbances such as pathogens (Cherubini *et al.* 2002) or defoliation (Morin 1994; Simard and Payette 2001).

In order to mitigate these limitations and to prevent underestimation of year of death, many authors have stressed the importance of collecting multiple increment cores at a given height or even a complete disc when crossdating dead trees (Amoroso and Daniels 2010; Jones and Daniels 2012; Bigler and Rigling 2013). However, the effect of the height at which samples are collected has received much less attention.

The overall objective of this study was to assess whether there is a time lag between the YOLRP in the lower and the upper part of dead trees in four of the main boreal species in eastern North America: trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* [L.] Mill.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* [Mill.] BSP). If present, the secondary objectives were to document the occurrence and the range of these lags while assessing if tree age at time of death and growth pattern exhibited in dying trees influenced the magnitude of the observed time lag.

METHODS

Study Area

The study was conducted in northwestern Quebec, at the transition between the mixedwood and coniferous boreal forest. Two distinct areas were sampled. For balsam fir, trembling aspen and jack pine, sampling was conducted in the Lake Duparquet Research and Teaching Forest (LDRTF), located 45 km northwest of Rouyn-Noranda (48°26′–48°29′N, 79°26′–79°18′W). The area is located in the Rouyn-Noranda ecological region, within the balsam fir-white birch (*Betula papyrifera* Marsh.) bioclimatic domain (Robitaille and Saucier 1998), where associations of balsam fir, black spruce, white spruce, paper birch and trembling aspen dominate. Disturbance history includes recurrent fires (Dansereau and Bergeron 1993), with spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks when fire cycle is long enough for host conifers to dominate the landscape (Morin *et al.* 1993).

For black spruce, sampling was conducted in the coniferous boreal forest, 120 km further north (49°25′–49°50′N, 79°18′–78°41′W), in the Lake Matagami Lowland ecological region, within the black spruce–feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) bioclimatic domain (Robitaille and Saucier 1998). Disturbance regime is characterised by large stand-replacing fires (Bergeron *et al.* 2004) with return intervals long enough for successional paludification processes to take place, organic deposits to build up and low productive, open forests to develop (Simard *et al.* 2007).

All stands were mature to late-successional. Stand age, past disturbance history and stand dynamics indicate that mortality causes were different among species (see Angers *et al.* (2010) for details). In balsam fir, mortality was caused by the 1970–1987 spruce budworm outbreak (Morin *et al.* 1993). In jack pine, most snags were recruited via competition and self-thinning mortality. Trembling aspen mortality was also related to self-thinning, but senescence and defoliation by the forest tent caterpillar (*Malacosoma disstria* Hbn.) possibly also played a role. Most black spruce deaths were presumably caused by senescence, although the last spruce budworm outbreak may have triggered some deaths (St-Denis *et al.* 2010).

Data Collection

Data collection was carried out during summers of 2004 and 2005 as part of a larger study on snag dynamics. Seventeen stands were selected based on species composition, soil type, drainage and age. Site selection was further constrained by accessibility and by absence of or very few harvesting activities based on historical reconstructions (Bescond 2002; Lecomte *et al.* 2006). In LDRTF, sites were mesic, slope was null to moderate (maximum 12%) and soils composed of glaciolacustrine clay. Black spruce sites were subhydric, characterised by a flat topography and soils composed of glaciolacustrine clay overlain by a thick (20–60 cm) organic layer.

In each stand, a 20 m × 20 m plot was established randomly, at least 50 m from any edge (road, cut, different stand). All snags (trees without green foliage with diameter at breast height (DBH) $\geq$ 5 cm) were characterized, as well as all logs from which the stump was identified within the plot (DBH $\geq$ 5 cm). Additional snags were sampled in the surroundings of the plots to increase sample size in some specific decay classes for a previous study (see Angers *et al.* 2012a,b). All dead trees from which we could collect upper and lower discs on the same continuous bole were considered for this study. Fragmented dead trees were discarded in order to avoid collecting discs on corresponding snapped tops on the ground that might have fallen before tree death.

Snags were felled and discs were taken from all dead trees that were sound enough to suggest potential use for dendrochronology analyses. Fragile samples were taped with thread-enforced tape and cut using a fine-toothed bow saw to hinder fragmentation. To optimise chances of successful crossdating, three discs were taken from each bole when possible: at base height (30 cm), breast height (1.3 m) and in the upper part of the tree, usually in the middle part of the crown.

Tree-Ring Analysis

All discs were dried and sanded with successively finer sanding paper until tree rings were clearly visible. When necessary, hot glue was used to consolidate fragmented samples prior to sanding. Samples were first examined to detect partial cambial mortality and to ensure that the two radii to be measured would capture the last ring formed. Ring width was measured for each disc along two radii (one when decay impeded ring visibility elsewhere on the disc) using a Velmex micrometer (precision of 0.001 mm, Velmex incorporated, Bloomfield, New York, USA). When partial cambial mortality occurred, we still measured the second radii, even if incomplete towards most recent years, to validate crossdating.

Each individual ring width series generated by all discs was crossdated against master series built for balsam fir, jack pine and trembling aspen from nearby living trees in LDRTF (Angers *et al.* 2010) and from a master chronology built for black spruce by Simard *et al.* (2007). Crossdating was performed using marker years of the premortality period, and with COFECHA (Holmes 1983) and TSAP (Rinn 1996) programs, the latter being used for visually comparing the pattern generated by each series and the average of the master series. This crossdating procedure established the YOLRP.

Data Selection and Analysis

Of the 363 dead trees detected in the field, only 145 were retained for this study. The 218 other dead trees were rejected for one or another of the following reasons: (1) to make sure that the time lags reported in this study were solely caused by real interruptions of cambial activity; we only retained discs for which we were confident that we captured the last ring produced (no decay or eroded wood), (2) discs sampled in the upper part of dead trees sometimes contained too few rings for reliable crossdating and were discarded, and (3) we only retained trees for which we had reliable crossdating discs sampled both in the upper and lower (stump and/or breast height) parts. The final sample consisted of 34 dead trembling aspens, 46 dead balsam firs, 26 dead jack pines and 39 dead black spruces. In 43% of the dead trees, we could only retain 2 discs (one in the upper bole and another one at either the base or breast height).

For each stem, the time lag was calculated as the difference between YOLRP in the upper (UP) and lower parts of trees (base height, BaH; breast height, BrH). This also allowed assessing if, as expected, missing rings prior to death were more frequent in the lower part than in the upper part of dead trees and, by extension, if these missing rings are more frequent at the base of trees than at breast height, *i.e.* if a 1 m difference in sample collection location indeed had an influence on results.

To assess if growth pattern of dying trees leads to time lags in YOLRP, we used an indicator of decline, hereafter referred as G10 slope. Simple linear regressions were applied to mean growth (ring increment of one or two radii measured per discs) of the 10 last rings produced in all discs sampled in the upper part of trees. These slopes were used to assess the way trees died: the larger the value of G10 slope, the more sudden the decline in growth preceding death.

Tree age has been shown to influence lag time (Bigler and Rigling 2013). For each tree, age was measured as the maximal number of rings from discs taken at the base of trees. When stumps were hollow, we estimated the number of missing rings based on averages obtained from discs taken at the base of trees of the same species where all rings were visible.

Mean comparisons were performed using one-way analysis of variance (ANOVA) and Tukey's HSD *post hoc* tests with log-transformation when needed to meet the assumptions of homoscedasticity and normality. However, variance was often intrinsically heterogeneous between species, and transformations could not satisfy basic assumptions. We therefore used non-parametric Kruskal-Wallis tests in these cases.

To assess the influence of G10 slope and age on magnitude of lag time between UP-BaH and UP-BrH, we first ensured that these two variables were not correlated using the Pearson's correlation coefficient. Correlations between age and growth preceding death when species were considered individually were very weak (all Pearson's r ≤ 0.13). We thus conducted multiple linear regressions. We expected that the growth pattern in the last years of ring production and, by inference, causes of mortality, might influence the response in time lags observed, with individuals experiencing a sudden decline in growth presenting no or short time lags and trees experiencing slower decline presenting longer time lags. Based on results from Bigler and Rigling (2013), we also expected older trees to exhibit longer time lags. All statistical analyses were performed using JMP 4.0.2 (SAS Institute, 2002).

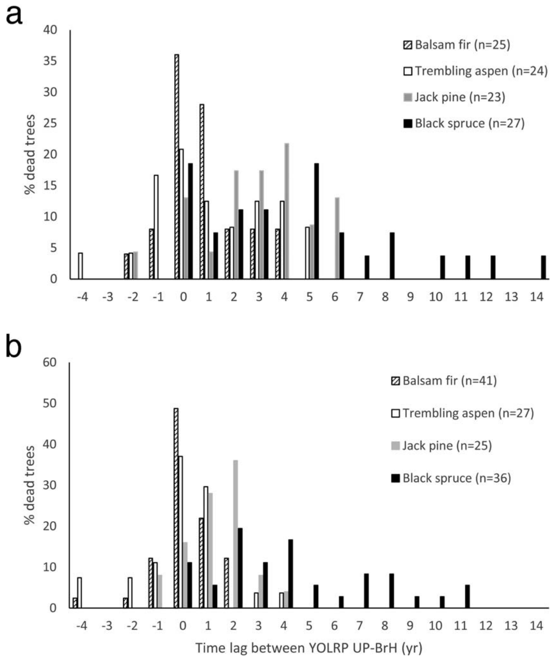

Figure 1. Time lag between year of last ring production (YOLRP) in the (a) upper part and at base height (UP-BaH) and (b) upper part and at breast height (UP-BrH) of dead trees in four boreal species.

In some dead trees, negative time lags were observed, indicating that growth was still occurring in the lower part of the trees while it had ceased in the upper part. Mechanisms underlying this phenomenon are different than for positive time lags and will be addressed separately. We thus computed statistics for positive time lags independently of negative time lags.

RESULTS

Occurrence and Range of Positive Time Lags

When considering null and positive time lags for all species, for UP-BaH as well as UP-BrH, more than half the time lags departed from zero (Figure 1), which indicated that discrepancies between YOLRP in the upper and lower part of the stem were common in our study area. Almost all species also showed longer and more variable mean time lags as well as a wider range of time lags between

Table 1. Time lag between year of last ring production in the upper and lower parts of dead trees (UP-BaH and UP-BrH) in four boreal species exhibiting null or positive time lags.

	UP-BaH (yr)			UP-BrH (yr)		
Species	*n*	Mean ± SD	Range	*n*	Mean ± SD	Range
Balsam fir	22	1.1 ± 1.3aA[§]	0–4	34	0.6 ± 0.7bA[§]	0–2
Trembling aspen	18	2.1 ± 1.8aA	0–5	20	0.8 ± 1.1bA	0–4
Jack pine	22	3.1 ± 1.9aAB	0–6	23	1.5 ± 1.0bA	0–4
Black spruce	27	4.6 ± 4.0aB	0–14	36	4.3 ± 3.2aB	0–11

[§] Different lower-case letters indicate significantly different values among time lags (UP-BaH and UP-BrH) for a given species whereas different upper-case letters indicate significantly different values among species for a given time lag. $p < 0.05$.

UP-BaH than UP-BrH (Table 1) except for black spruce that exhibited statistically similar time lags ($p = 0.7269$). This indicates, as expected, that missing rings are usually more frequent at the base of trees than at breast height.

The distribution and range of null and positive time lags varied across species (Figure 1), with mean UP-BaH time lags of 1.1 to 4.6 years and ranges extending from 4 to 14 years (Table 1). Despite an apparently more concentrated distribution on very short time lags in balsam fir (73% of UP-BaH lags and 85% of UP-BrH lags were 0 or 1 year) than trembling aspen or jack pine, mean time lags were statistically similar in the three species (Table 1). However, black spruce showed a different pattern, with time lags that were longer (mean time lag of more than 4 years for both UP-BaH and UP-BrH) and covered a wider range (UP-BaH time lags extended up to 14 years). Black spruce mean time lag values were significantly different from all other species except for jack pine UP-BaH.

Unexpectedly, up to 26% of lags were negative and were observed in all species but black spruce, mostly in trembling aspen (Figure 1). Lags between YOLRP UP-BaH were mostly −1 or −2 years but reached −4 years in one trembling aspen individual.

Effects of Age and Growth Preceding Death

Species sampled at LDRTF (balsam fir, trembling aspen, jack pine) showed similar mean age at death of 50–64 years whereas black spruce trees from old-growth forests died at a mean age of 172 years (Table 2). Mean G10 slope was more variable between species, from balsam fir exhibiting steep decline in growth preceding death ($m = -87.7$, Table 2) to black spruce showing the opposite trend with a very slow decline ($m = -7.4$) while trembling aspen and jack pine were in an intermediate position ($m = -68.2$ and -41.3, respectively).

Multiple linear regressions of the effects of age and growth preceding death on individual species showed that in jack pine and black spruce, neither age nor G10 slope influenced time lag magnitude (Figure 2; $p = 0.2139$ and 0.3597, respectively). In balsam fir, time lags tended to be slightly longer when trees were older ($p = 0.0173$). Trembling aspen was the only species to exhibit a significantly positive relation between G10 slope and YOLRP UP-BaH when considering the two individuals that experienced extremely abrupt declines ($p = 0.0208$, $p = 0.1057$ without these outliers).

This general absence of relationships in most species might, however, be related to the low

Table 2. Slope of growth in the 10 years preceding death (G10 slope) and age in four boreal species exhibiting null or positive time lags.

	G10 slope			Age (yrs)	
Species	*n*	Mean ± SD	Range	Mean ± SD	Range
Balsam fir	18	−87.7a	30.1 to −196.1	60.4 ± 14.0a	32–92
Trembling aspen	17	−68.2ab	−4.0 to −308.0	64.2 ± 11.8a	44–82
Jack pine	21	−41.3bc	−8.8 to −88.7	50.4 ± 11.4a	35–73
Black spruce	25	−7.4c	−1.9 to −54.2	171.5 ± 31.4b	125–247

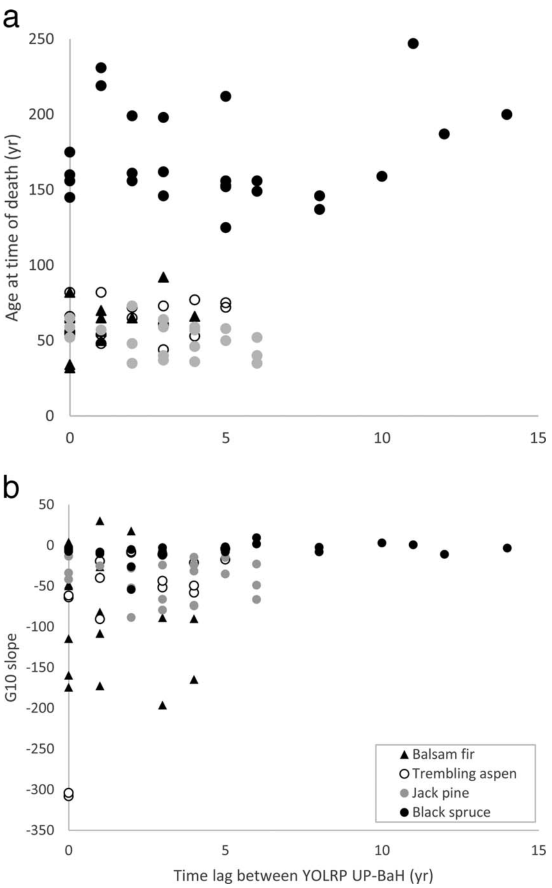

Figure 2. Time lag between YOLRP UP-BaH (yr) in relation to (a) age at time of death and (b) slope of the 10 years of growth preceding death (G10 slope) in four boreal species exhibiting null or positive time lags.

variability in age and G10 slope of sampled trees within a given species (Figure 2, Table 2). In order to have a wider range of age and G10 slope and possibly detect some general trends, we plotted and analysed data from all species combined, even though we recognize that merging species may be challenging because many internal and external factors are not considered (Figure 2). When doing so, age and G10 slope showed a significant level of correlation (Pearson's $r = 0.39$, $p = 0.0004$). We thus considered the two factors separately. When considering all species together, a general pattern emerged in which larger time lags were observed in trees experiencing slower declines in growth (G10 slope near 0; $p = 0.0046$) and in older trees at time of death ($p = 0.0004$).

DISCUSSION

Occurrence and Range of Positive Time Lags

In living trees, the frequency of discontinuous or missing rings have been shown to be highly negatively correlated to sample height in white pines (*Pinus strobus* L.) undergoing suppression (Bormann 1965) and Aleppo pines (*P. halepensis* Mill.) living in a semiarid environment (Novak *et al.* 2011). However, Novak *et al.* (2011) found no significant relation in stone pine (*P. pinea* L.).

In dead trees, very few studies have documented discrepancies between YOLRP at different heights because, most of the time, cores are collected at the same height. We only found two studies reporting this phenomenon, both conducted in the Swiss National Park on mountain pines (*Pinus mugo* Turra). Cherubini *et al.* (2002) compared YOLRP of cores collected at 20 cm and 1 m and found positive lags in YOLRP ranging from 1 to 17 years between the two heights (Cherubini *et al.* 2002; Cherubini personal communication). Bigler and Rigling (2013) compared YOLRP of cores collected at the base (*ca.* 36 cm) and at *ca.* 80 cm. They also found great variability in the lags, with positive lags (*sensu* this study) up to 30 years between the two heights. Both studies observed positive and negative time lags and presented distributions skewed towards positive lags, as in this study, and reported that about 80% of trees exhibited different YOLRP between the two heights. In our study, we report differing YOLRP in 64–87% of trees according to species for much greater distances between the two samples (Up-BaH).

Large discrepancies at such a small distance reported by Cherubini *et al.* (2002) and Bigler and Rigling (2013) are likely in part attributable to the fact that crossdating was performed on increment cores (one core per height in the case of Cherubini *et al.*; one at the base and two at *ca.* 80 cm in Bigler and Rigling), which limited the potential to capture incomplete growth rings because of partial cambial mortality of some parts of the boles. To our knowledge, by basing our results on relatively well-conserved and complete discs, our study is unique in that we overcame the crossdating shortcomings of partial cambial mortality related to core sampling and degradation of the outermost rings. This enabled us to have great confidence in the representation of difference in YOLRP at different heights.

Effects of Age and Growth Preceding Death

Of the four species studied, none had the same stand, stress, or disturbance history. Species-specific physiological response to disturbances or limitations in resources obviously played a role in the observed results. Our study design thus did not allow assessing and discriminating the relative influence of species from agents and events leading to death. However, interesting general trends were observed.

For most species considered individually, we found no relationship between YOLRP UP-BaH and age nor G10 slope. This result is likely attributable in part to the relative homogeneity in stand history and presumed causes of mortality affecting a given species that induce relatively little heterogeneity in age and growth decline among individuals.

For example, the vast majority of balsam fir experienced severe defoliation by the spruce budworm causing widespread mortality. Most balsam fir tree deaths were likely the result of this stress that triggered sudden declines in growth, translated into steep G10 slopes, and the narrowest range of time lags observed among species (Tables 1 and 2). The black spruce sample, on the contrary, showed very gentle and gradual G10 slope declines resulting in the longest time lags. In this species, growth is already very slow (increment less than 1 mm yr^{-1}) because of the poor, paludified organic soils (Simard *et al.* 2007). The only species that seems to have experienced contrasting causes of death is the trembling aspen, with two individuals from two different sites exhibiting especially abrupt declines with no indication of particular causes of death.

Despite the aforementioned limitations of grouping species, combining all observations suggests that trees that are old or that experience gentle G10 slope do not necessarily experience long time lags. However, trees that do exhibit longer time lags are old and slowly declining individuals.

To conclude on the effects of age and growth preceding death on the magnitude of time lags, one should implement a sampling design for the study of a single tree species, which would be aimed at contrasting causes of mortality for different contexts. These contrasting causes should range from ephemeral and severe disturbances (such as severe defoliation or drought) to persistent over the long-term but less severe stresses (such as competition, self-thinning and senescence).

"Living Snags"

We expected year of death to be in some cases underestimated when sampling the lower part of dead trees, but the opposite response was counterintuitive, *i.e.* negative time lags, indicating that secondary growth was going on in the lower part of the bole whereas it had stopped in the upper part. Negative time lags were likely caused by early crown death while trees had sufficient reserves to maintain growth in the lower bole. Although it is not well documented, Bormann (1966) reported this phenomenon as early as 1966, referring to dead trees experiencing stump growth as "living snags".

In conifers experiencing severe defoliation, several authors reported a delayed growth response between the upper and lower parts of the stem, with a marked reduction of ring width in the upper part of the stem at the beginning of the outbreak, which was only noticeable later in the lower part of the stem (see Krause *et al.* (2003, 2012) for a review). In mature balsam firs, Krause and Morin (2003) observed such delays ranging from zero to three years. They suggest that reserves stored in the roots and at the stem base might be sufficient to ensure growth for such a period in the lower part of the tree. However, they only studied trees that survived a spruce budworm outbreak. Our growth patterns in severely defoliated dead balsam fir suggest that it is possible that death occurred when growth had ceased in the upper part of the stem while the lower part survived for a short period of time supported by stored reserves, because these trees never recovered.

The mechanism is likely different in trembling aspen and jack pine. Indeed, these species are known to be interconnected to neighboring conspecifics via roots. Stumps of seemingly dead trees (absence of green foliage in the crown) can therefore be supplied with carbohydrates from living grafted trees. Most studies reporting "living stumps" of grafted trees were conducted following partial cutting or girdling for an array of coniferous species (Bormann 1961; Lanner 1961; Eis 1972; Tarroux *et al.* 2010), including jack pine. Secondary growth of living stumps was reported to last for several years (Tarroux *et al.* 2010), even up to decades (Lanner 1961; Eis 1972) and to occur up to 3 m in height (Lanner 1961; Bormann 1966), well beyond the usual height where cores are collected for crossdating purposes. In jack pine stands sampled in our study area, Tarroux *et al.* (2010) found that grafted stumps lived on average 2 years after being cut, with some stumps still living after 9 years.

It can be hypothesised that because they are alive at time of harvest, cut trees are physiologically capable of secondary growth if supplied by their root system or through root grafts. However, in trees that died after experiencing deprivation of resources (self-thinning, defoliation, drought, etc.), one might expect that they would lose this ability. Yet, although less documented, Bormann (1966) observed "living" white pine snags, *i.e.* snags that were still producing annual rings in the lower part of the bole many years after they were considered dead based on the absence of green foliage, thanks to root grafting.

In trembling aspen, trees are prone to experience crown dieback, where the upper part of the crown is seemingly dead while green foliage remains in the lower part until the tree dies entirely. This gradual top-to-bottom death might explain that 25% of dead aspens exhibited a negative UP-BaH time lag. To our knowledge, however, this has not been documented in the literature. Desrochers and Lieffers (2001) and Jelínková *et al.* (2009) documented survival and growth in roots of dead stumps for many years, but did not report evidence of secondary growth at stump height. Trembling aspen has a clonal root system and is more prone to suckering than jack pine, so it is thus possible that resources of the living root system of dead trees are primarily allocated to living trees or new suckers, but the relatively frequent occurrence of negative time lags in our study suggest that stumps of snags might be supplied by their individual remaining resources or by intraclonal living ramets or grafted trees for some time.

Implications for Sampling Dead Trees

Using dendrochronological crossdating to retrospectively date the death of trees can be biased and lead to underestimation of the year of death as compared to field observations because physiological activity of the crown, observable by the presence of green foliage, can occur even if growth has ceased. The discrepancies between these two ways to evaluate year of death are highly variable. Mast and Veblen (1994) reported a 1–3 years difference in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) stands, Jones and Daniels (2012) measured an average discrepancy of 3.3 years in white spruce (*Picea glauca* [Moench] Voss) and 10 years in lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.), and Bigler and Rigling (2013) and Cherubini *et al.* (2002) observed differences of up to 15 and 31 years, respectively, in mountain pine. Consequently, many authors have emphasized the need to validate dendrochronological dating of tree deaths with field observation of the trees in permanent sample plots and to build correction models to improve the accuracy of dating (Jones and Daniels 2012; Bigler and Rigling 2013).

The results of this study suggest that it is possible to at least reduce this underestimation of actual year of death by sampling discs in the upper part of boles. This procedure is however destructive and more time consuming. The decision of selecting this option must therefore rely on a serious evaluation of the sampling cost-benefit ratio by examining the research objectives, the level of accuracy and precision required, and the prevalence and magnitude of time lags in a given situation.

We found that collecting samples only 1 m higher (*i.e.* at BrH instead of BaH) significantly enhanced the accuracy of year of death estimates for most tree species. When first growth rings from the stump are not required (for instance to assess the age of trees more precisely), sampling at BrH usually represents a good estimate of actual YOLRP for a similar sampling effort. Sampling at BrH also reduces the occurrence of negative time lags that generate overestimation of year of death.

In black spruce, however, the gain is small (mean difference of 0.3 year between UP-BaH and

UP-BrH), but the mean time lag is still large (more than 4 years). Our results suggest that old individuals and trees that experience slow decline are the most likely to show longer time lags. In these cases, it would be most useful to collect discs in the upper part of the bole to ensure capture of the last ring produced. When there is some doubt, pre-sampling can be employed to devise an effective sampling procedure.

The results of this study underline the importance of understanding the dynamics of the stand to be sampled when selecting a sampling procedure to reconstruct temporal mortality patterns. Age of trees, growth preceding death, and, by extension, type of disturbance are all factors that may affect the probability to capture the last ring produced and the magnitude of time lags between sampling heights. Our results suggest that stands with great heterogeneity in these factors are probably more prone to include individuals showing large time lags. For example, first cohort, even-aged stands that experienced severe disturbances are probably less likely to display large time lags than old-growth, uneven-aged stands in which mortality is mostly attributable to stand-development processes such as competition and senescence.

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